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A phytosociological survey of aquatic vegetation in the main freshwater lakes of Greece

Dimitrios Zervas^{1,2}, Ioannis Tsiripidis¹, Erwin Bergmeier³, Vasiliki Tsiaoussi²

- 1 Department of Botany School of Biology, Aristotle University of Thessaloniki, Greece
- 2 Greek Biotope/Wetland Centre (EKBY), The Goulandris Natural History Museum, Thessaloniki, Greece
- 3 Department of Vegetation and Phytodiversity Analysis, University of Göttingen, Germany

Corresponding author: Dimitrios Zervas (dzervas@ekby.gr)

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Abstract

Aims: This study aims to contribute to the knowledge of European freshwater lake ecosystems with updated and new information on aquatic plant communities, by conducting national-scale phytosociological research of freshwater lake vegetation in Greece. Moreover, it investigates the relationship between aquatic plant communities and lake environmental parameters, including eutrophication levels and hydro-morphological conditions. **Study area:** Lakes in Greece, SE Europe. Methods: 5,690 phytosociological relevés of aquatic vegetation were sampled in 18 freshwater lake ecosystems during 2013–2016. The relevés were subjected to hierarchical cluster and indicator species analyses in order to identify associations and communities of aquatic vegetation, as well as to describe their syntaxonomy. Multiple regression analysis was applied to investigate the relationship between vegetation syntaxa and environmental parameters of lakes, i.e. physico-chemical parameters and water level fluctuation. **Results:** Ninety-nine plant taxa belonging to 30 different families were recorded. Forty-six vegetation types were identified and described by their ecological characteristics, diagnostic taxa and syntaxonomical status. Thirteen vegetation types, the largest number belonging to the vegetation class *Charetea*, are considered to be new records for Greece. The distribution of the vegetation types recorded in the 18 freshwater lakes was found to depend on environmental parameters and levels of eutrophication. Conclusions: An updated aquatic vegetation inventory was produced for Greek lakes, and primary results showed that the presence/ absence of aquatic plant communities and the community composition in freshwater lakes can be utilized to assess the pressure of eutrophication on lake ecosystems.

Taxonomic reference: Euro+Med (2006–).

Abbreviations: MNT = Mean number of taxa; WFD = Water Framework Directive.

Keywords

aquatic plant, charophyte, ecological status, eutrophication, Greece, lake, macrophyte, phytosociology, plant community, vegetation

Introduction

Freshwater ecosystems are among the most threatened ecosystems around the world (Sala et al. 2000; Foley et al. 2005; Dudgeon et al. 2006). Overexploitation, water pollution, flow modification, destruction or degradation of habitats, and exotic species invasions are the five

main drivers of biodiversity loss in freshwater ecosystems (Dudgeon et al. 2006). The European Union addressed the vulnerability of freshwater ecosystems with the adoption of the European Water Framework Directive (WFD, European Commission 2000). In this frame-



work, the monitoring of aquatic plant communities was proposed as a key element in order to assess the ecological status of freshwater ecosystems, as macrophytes play a significant role in determining the structure and functions of lake ecosystems by influencing environmental conditions, nutrient cycling, and biotic assemblages and interactions (Carpenter and Lodge 1986; Jeppesen et al. 1997; Engelhardt and Ritchie 2001). As a result, most of the monitoring and assessment systems developed by European countries utilise rankings in the tolerance and sensitivity of macrophyte taxa to eutrophication (Kolada et al. 2014; Poikane et al. 2018). The monitoring of aquatic macrophytes in Greek freshwater ecosystems, in the context of the Greek National Water Monitoring Network (GNWMN) under the WFD, began in 2013 (Zervas et al. 2018).

The number of floristic and phytosociological investigations in freshwater ecosystems within Greece has increased during the past three to four decades (Sarika-Hatzinikolaou et al. 2003; Sarika et al. 2005). Also publications containing phytosociological data for lacustrine aquatic plant communities have accumulated over time, but remain scarce and not evenly distributed across the country: Gradstein and Smittenberg (1977: western Crete), Lavrentiades and Pavlidis (1985: Lake Mikri Prespa), Papastergiadou (1990: various lakes in Northern Greece), Bergmeier (2001: seasonal pools in the island of Gavdos), Sarika-Hatzinikolaou et al. (2003: seven lakes in Epirus), Grigoriadis et al. (2005: Agras wetland), Dimopoulos et al. (2005: Kalodiki marsh); Zotos (2006: Lakes Trichonida and Lysimachia), Fotiadis et al. (2008: Lake Chimaditida), and Pirini (2011: Lakes Vegoritida and Petres). These studies provide important information about aquatic vegetation in Greece, but the older ones do need to be revised and updated. Furthermore, research

gaps remain in the country, i.e. a number of important lakes remain unsurveyed.

Taking into consideration all of the above information, the main objectives of this study are (i) to contribute to the knowledge of European freshwater lake ecosystems with new and updated country-wide information on the aquatic plant communities found in the main Greek freshwater lakes, and (ii) to investigate the relationship between the distribution patterns of macrophyte communities and environmental parameters indicating increased levels of eutrophication and altered hydro-morphological conditions.

Study area

The study covers 18 lakes (Table 1; Figure 1) selected for GNWMN monitoring of aquatic macrophytes (Mavromati et al. 2017; Zervas et al. 2018). While the studied lakes are scattered over the Greek mainland, most of them are clustered in the west and north-central part of the country, differing in altitude, size, water depth, and local climatic conditions within their catchment area (Table 1). Of the three transboundary lakes (Doirani, Megali Prespa, Mikri Prespa) only their Greek areas were studied.

Methods

Vegetation and environmental data

Each lake was surveyed once in 2013–2016 during the main growing season (May to September) (Table 1). In all lakes, the belt transect-mapping method was applied

Table 1. Overview of the geographical, geometric and climatic characteristics of the studied lakes. Asterisks mark transboundary lakes, for which the characteristics refer to their part in Greece. Climatic characteristics have been collected by the European Climate Assessment & Dataset (Klein Tank et al. 2002). Average annual temperature and annual precipitation values have been calculated on the basis of available data during the period 1995-2005. Survey period and number of transects and relevés surveyed per lake is also given.

No	Lake	Centroid Latitude (°N)	Centroid Longitude (°E)	Mean Altitude (masl)	Area (km²)	Mean-Max depth (m)	Aver. Annual Temp. (°C)	Annual Preci- pitation	Climate zone (Köppen &	Survey period	No of transects/ relevés
								(mm)	Geiger)		recorded
1	Volvi	40.67740	23.47368	37	75.5	13-28	15.6	458	Csa	Aug 2016	20 / 317
2	Doirani*	41.23853	22.76487	146	30.7	4-8	14.3	453	Cfa	Aug 2016	10 / 173
3	Vegoritida	40.74464	21.78442	517	46.5	25-52	11.5	530	Cfb	June 2016	20 / 509
4	Petres	40.72604	21.69612	573	12	3-6	11.5	562	Cfb	June 2016	16 / 227
5	Zazari	40.62507	21.54690	600	3	5-8	11.5	595	Cfb	July 2016	12 / 124
6	Chimaditida	40.59258	21.56585	592	9.1	1-5	11.5	595	Cfb	July 2016	16 / 239
7	Kastoria	40.52269	21.30080	627	31.2	4-9	11.4	697	Cfb	Aug 2014	20 / 312
8	Megali Prespa*	40.85057	20.98875	845	39.4	~16-26	10.2	750	Cfb	Aug 2015	12 / 206
9	Mikri Prespa*	40.77031	21.10128	850	46.7	4-10	10.2	728	Cfb	Aug 2015	15 / 294
10	Pamvotida	39.66270	20.88518	469	22.6	5-12	13.2	1081	Csa	Sept 2013	20 / 74
11	Amvrakia	38.75113	21.17941	20	13.5	22-54	17.3	930	Csa	June 2014	20 / 331
12	Ozeros	38.65358	21.22294	24	10.5	4-7	17.2	931	Csa	June 2014	20 / 178
13	Lysimachia	38.56234	21.37665	15	13	4-8	17.1	909	Csa	June 2014	20 / 215
14	Trichonida	38.57309	21.54813	16	93.4	30-56	17.1	902	Csa	July 2015	20 / 792
15	Paralimni	38.45862	23.35285	37	10.6	5-8	17.5	527	Csa	July 2014	20 / 503
16	Yliki	38.39764	23.27973	75	22.5	22-34	17.5	527	Csa	July 2014	20 / 29
17	Feneos	37.92861	22.28513	872	0.5	10-29	11.5	862	Csb	Aug 2014	10 / 373
18	Kourna	35.33180	24.27776	16	0.6	~15-22	18.2	831	Csa	May 2014	14 / 794



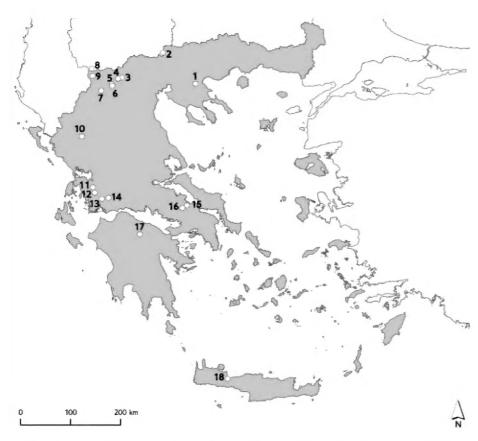


Figure 1. Map of the surveyed Greek freshwater lakes. See Table 1 for lake names.

(Zervas et al. 2018), the most commonly used method for aquatic vegetation surveys in Europe, due to the fact that it provides abundance, frequency and depth distribution data for the different taxa found within the vegetation of a lake (Kolada et al. 2009). Ten to 20 transects per lake were established from the shoreline perpendicular to the maximum depth of plant growth. Sampling was conducted in relevés of 4 m², evenly distributed along the belt transects following a gradient of increasing depth. Sampling was undertaken using a double-headed rake with a scaled handle or attached to a rope, a bathyscope, and a geo-bathymetric device. In this way, a total of 5,690 relevés were sampled, in which all angiosperms (helophytes, hydrophytes, amphiphytes and aquatic forms of land species), pteridophytes, bryophytes, charophytes and green filamentous macroalgae (e.g. Cladophora spp.) were recorded and determined to species or subspecies level (except filamentous macroalgae), and their abundance was estimated with the use of the semi-quantitative five-point DAFOR scale (Palmer et al. 1992). Vascular plant taxonomy follows Euro+Med (2006), while algae taxonomy follows Guiry and Guiry (2019). Chorological information was collected from Dimopoulos et al. (2013, 2016), Guiry and Guiry (2019), and Julve (1998).

A number of environmental data (e.g. total phosphorus concentrations in the water column, Secchi depth, water electric conductivity, water level fluctuation measurements) were collected periodically from each lake in the context of GNWMN (for details see Zervas et al. 2018). These data were used to assess the relationships between the distribution patterns of aquatic syntaxa and eutrophication and hydro-morphological factors.

Statistical analysis

In order to define the vegetation types in the most objective manner possible, the relevés were subjected to a

number of hierarchical cluster analyses. Extremely rare taxa, i.e. recorded in one to three out of 5690 plots, were excluded from the analyses in order to reduce "noise" in the data. DAFOR abundance classes were translated to their average percentage abundance values as follows: Dominant = 87.5%, Abundant = 50%, Frequent = 17.5%, Occasional = 5.5% and Rare = 0.5% (CEN 2007). Species abundances were chord distance-based transformed (Legendre and Galacher 2001). The transformed dataset was then subjected to cluster analysis with the use of flexible beta linkage method with b = -0.25 (Lance and Williams 1967) and Bray-Curtis dissimilarity (Bray and Curtis 1957). Elbow and Average Silhouette methods (Kaufman and Rousseeuw 1990), and NbClust statistic (Charrad et al. 2014) were used to assist in the determination of the optimal number of clusters for the dataset. Finally, diagnostic taxa were determined by indicator species analysis (Dufrene and Legendre 1997; De Cáceres et al. 2012), using the indicators function, in order to finalize the number of clusters corresponding to distinct vegetation types, and describe the best combination of indicator species for each vegetation type.

Due to the overall low number of common taxa among the resulting clusters, the hierarchic dendrogram that was produced was not able to successfully group all vegetation types into meaningful syntaxa, thus we proceeded with an additional cluster analysis. The synoptic table, which contained the clusters representing our dataset, was integrated into a dataset of clusters representing the types of Greek aquatic vegetation published in the past (bibliography in Suppl. material 1) and was processed again using the flexible beta linkage method and Bray-Curtis dissimilarity. The aim of including these vegetation types from the literature within our dataset was to support the present syntaxonomical decisions. The syntaxonomy of higher syntaxa (alliances, orders and classes) in the current study follows, with few exceptions, Mucina et al. (2016).

Depth distribution for each vegetation type was calculated and presented. The distribution of higher-rank syntaxa for each lake was also computed on the basis of the number of relevés per syntaxon in proportion to the total number of relevés in each lake. Calculations were summarized at the level of class for most of the vegetation types, except the ones belonging to the *Potamogetonetea* which were divided at the level of alliance, owing to the high variation in this class with different life forms. Finally, a multiple linear regression model was applied to assess the relation between aquatic vegetation patterns, as expressed by the abundance of higher-rank syntaxa, and environmental parameters in each lake. Pearson's correlation coefficient (*R*) and p-value (*p*) of the model were assessed.

All analyses were performed with the use of vegan (Oksanen et al. 2018), cluster (Maechler et al. 2018), factoextra (Kassambara and Mundt 2017), NbClust (Charrad et al. 2014), indicspecies (De Cáceres and Legendre 2009), and tidyverse (Wickam 2017) R packages in R environment version 3.5.2 (R Core Team 2018).

Results and discussion

Species composition

The total number of taxa (vascular plants and macroalgae species) recorded in the studied lakes was 99. The most species-rich among the 30 different plant families were Characeae (12%), Cyperaceae (12%) and Potamogetonaceae (10%), followed by Hydrocharitaceae (7%), Lamiaceae (6%) and Poaceae (6%). Hydrophytes were the dominant life form (55% of total species) followed by hemicryptophytes (25%) and geophytes (19%). The most prominent chorological element was the Cosmopolitans (26%), followed by Paleotemperates (15%), European-SW Asians (15%) and Circumtemperates (14%). Most of the taxa (80 out of 99) were recorded with frequencies of less than 1%, i.e. they were found in fewer than 57 plots out of all 5,690. The most frequent taxa (found in more than 500 plots) were Myriophyllum spicatum (29.3%), Phragmites australis (27.2%), Ceratophyllum demersum (25.1%), Vallisneria spiralis (23%), Stuckenia pectinata (22.5%) and Najas marina (14.3%). Twenty-six out of 99 taxa were recorded in three or fewer plots (taxon frequencies for each lake are summarized in Suppl. material 2).

Vegetation classification

Cluster analysis and subsequent tests resulted in 46 different vegetation types for interpretation (see Suppl. material 3 for Elbow, Average Silhouette and NbClust results, and Suppl. material 4 for produced dendrogram). Due to the survey methodology used, i.e. consecutive relevés distributed along a depth gradient at equal depth intervals, a number of the resulting vegetation types correspond to transitional ecotonal stands. These vegetation types were retained in the synoptic tables and are described in the text so as to present a more comprehensive picture of the spatial and ecological patterns of vegetation differentiation within the studied lakes. For syntaxonomic purposes, they may well be merged with an adjacent vegetation type. The diagnostic species for each vegetation type were selected from the results of the indicator species analysis as those combinations that reached a higher Indicator Value, while maintaining high prediction power and sensitivity (De Cáceres et al. 2012) (see Suppl. material 5 for all diagnostic taxa parameters). Diagnostic and accompanying species for each vegetation type are given in Tables 2-4. Short descriptions of the ecology (structure, water-depth preference etc.), the floristic composition and the distribution for each vegetation type are presented at the following paragraphs (see Suppl. material 6 for summary of vegetation types in all lakes). Syntaxonomic remarks that led to their final syntaxonomic assignment (Table 5) are also presented.

Class 1. Plantaginetea majoris

Syntaxon 1.1. *Phyla nodiflora* community (Code PhN, Table 2, Mean number of taxa MNT = 2.4)

Appearance and habitat: Sparse temporarily submerged carpets, dominated by *Phyla nodiflora*, a perennial herb of prostrate growth, covering periodically flooded shores. *Phyla nodiflora* is a cosmopolitan pioneer herb that grows prolifically in floodplain wetlands with periodical flooding of short duration (Sharma and Singh 2013). Other aquatic macrophytes rapidly colonizing flooded areas, such as *Myriophyllum spicatum* and *Vallisneria spiralis*, can also be found in this community.

Diagnostic taxa (% constancy): *Phyla nodiflora* (100%). Distribution: Amvrakia, Yliki.

Syntaxonomic remarks: No association dominated by Phyla nodiflora was found in the European literature. An association of Phyla nodiflora growing together with Kyllinga peruviana (Kyllingo-Phyletum nodiflorae Vanden Berghen 1990) (De Foucault et al. 2013) was described in West African temporarily inundated coastal dune slacks, another with Paspalum vaginatum (Lippio nodiflorae-Paspaletum vaginati Galán de Mera, Linares, Campos and Vicente 2009) in South American saltwater influenced grasslands on the Pacific coast (Galán de Mera et al. 2009). In publications from the western Mediterranean basin (e.g. Brullo and Sciandrello 2006; Ninot et al. 2011) an association of *Phyla nodiflora* growing in littoral grassy plains together with Panicum repens (Lippio nodiflorae-Panicetum repentis O. Bolòs 1957) has been described, but our community differs as Panicum repens is absent. Our material is insufficient to provide a firm basis for describing a new association. We do not follow Mucina et al. (2016) who treat the perennial *Phyla nodiflora* as a diagnostic species of the class Isoëto-Nanojuncetea, defined as pioneer ephemeral vegetation in periodically flooded freshwater habitats. We assign the *Phyla nodiflora* community described here to the order Paspalo-Heleochloetalia and to the alliance Paspalo-Agrostion semiverticillati instead, which comprises Mediterranean-subtropical temporarily inundated, disturbed, perennial grass-herblands rich in stoloniferous plants of tropical and subtropical distribution.

Syntaxon 1.2. *Paspalo distichi-Agrostietum verticillatae* (Code PD, Table 2, MNT = 3.1)

Appearance and habitat: Emerged and floating mats of *Paspalum distichum* colonizing exposed areas of wet ground that may be temporarily shallowly inundated. *Paspalum distichum* is a perennial grass, originating from tropical America, which is widely established in riparian habitats of the Mediterranean basin, often forming monotypic stands (Aguiar et al. 2005).

Diagnostic taxa (% constancy): Paspalum distichum (100%).

Distribution: Doirani, Lysimachia, Paralimni, Trichonida and Vegoritida.



Table 2. Synoptic table of the identified associations and communities belonging to Classes *Plantaginetea majoris*, *Phragmito-Magnocaricetea* and *Lemnetea*. Taxa constancy in percentage and their average abundance class (r = 0-1%, t = 2-5%, t = 6-20%, t = 21-40, t = 21-40,

Vegetation type code	PhN	PD	PA	PAE	SL	TD	TL	TA	BU	LM	UV	CD	CDE	CDMS
Number of relevés	5	22	1065	29	18	18	18	14	17	11	10	735	55	62
Mean number of species	2.4	3.1	1.2	3.4	5.6	3.1	2.3	2.1	4.5	5.8	5.2	1.5	3.5	2.6
PLANTAGINETEA														
Phyla nodiflora	100¹	5 ¹	1 r		6 ^r	•								•
Paspalum distichum	•	100¹			17¹					55¹	•	1 ¹		
PHRAGMITO-MAGNOCARICETEA														
Phragmites australis	•	14⁺	100⁴	97 ²	78¹	842	6 ^r	8 ¹	30¹	28¹	20⁺	11 ¹	64 ²	71
Schoenoplectus lacustris		5 ^r	1⁺		100 ²	•			•		20⁺	1 ¹		
Typha domingensis	•	10⁺	2 ¹	7 ¹	50 ²	100³	•		•	19¹	10¹	6 ¹	11⁺	
Typha latifolia	•	10¹	1⁺	21 ¹	6 ^r		100¹	8 ^r	•	19¹	204		4 ¹	
Typha angustifolia	•		11		61		61	100¹						
Butomus umbellatus			•					٠	100 ²					
Schoenoplectus litoralis			•						36 ¹					
Alisma plantago-aquatica	•			•		12¹			•	19 ^r	30 ²		2 ¹	
Carex pseudocyperus	•	•	11								30 ²			
Juncus subnodulosus											30¹			
Mentha aquatica	•	5 ^r		4 ¹	61						4O1	1+		
Lycopus europaeus	•	5 ^r	1 ¹		6 ^r		4 ¹	•	÷	19⁺	20 ¹	1 ¹		
Eleocharis palustris			1 ¹	4 ¹			6 ^r							
Stachys palustris				4 ¹		6 ¹					20 ¹		2 ¹	
Lythrum salicaria	•		•										4 ¹	
Rorippa amphibia	•		•	7⁺		•			•			•	4 ¹	
Oenanthe aquatica	•		•	4 ^r		•				28 ^r	•		2 ^r	•
Sparganium erectum	•	5 ¹			12 ¹									•
LEMNETEA														
Lemna minor	•	5 ¹	1 ¹	11 ²				•	•	100³	3O ²		17 ²	
Lemna gibba										46 ¹			4 ¹	
Azolla filiculoides	•		1 ^r	4 ^r						73 ¹				
Spirodela polyrhiza	•		1⁺	4 ¹						37 ¹		1⁺	15¹	
Salvinia natans	•		1 ¹	4٢		•	•		•	19 ²	•	•	15¹	•
Utricularia vulgaris + australis	•	•	1 ¹	4 ¹		•	•	•	•	•	100 ²	•	•	•
Ceratophyllum demersum	•	•	61	11 ¹	23¹	39 ³	•	•	•	28¹	•	100³	100 ²	100 ²
Ceratophyllum submersum	•	•	1 ¹			6 ¹	•	•	•			1 ¹	•	
Hydrocharis morsus-ranae	•	•	1⁺	4 ¹		12 ¹	•		•	10 ¹	40 ¹	•	171	
Other taxa														
Myriophyllum spicatum	60 ¹	10 ¹	3 ¹	14⁺	39 ¹		78¹	43⁺	100¹	10 ¹		8+	19⁺	100¹
Stuckenia pectinata			3 ¹	71	28⁺							3 ¹	19¹	9+
Vallisneria spiralis	60 ²	10⁺	2 ¹	7⁺	39⁺	341	•	•	831	•	•	71	13⁺	12 ¹
Potamogeton lucens	•	5 ¹	1 ¹			•	•		59 ¹			3 ¹	•	10¹
Rumex palustris	•	10 ^r	11	4 ¹	12⁺	•1)	• 10			372	201			
Potamogeton nodosus	20 ¹	10 ^r		•	17 ¹							1 ¹		5 ¹
Najas marina	•	5 ¹	3 ¹	18¹	231		•		61		10 ^r		10⁺	10⁺
Zannichellia palustris	•	•	1 ¹	4 ^r		•	•				20 ¹	•		•
Ludwigia peploides	•	231	2 ¹			•	•	•			•	1 ¹		•
Chara globularis	•	5 ¹	•			23 ¹	•	221	•		•	•	•	•
Cladophora glomerata	•	37⁺	1⁺	49 ¹	17¹	17¹	•	•	30⁺	37⁺	•	5⁺	13 ²	2 ^r
Nitellopsis obtusa	•			14 ³					•			1 ¹		

Taxa with less than 20% constancy: Juncus articulatus, SL:17¹; Mentha pulegium, TA:8¹; Eleocharis mitracarpa, UV:10¹; Potamogeton perfoliatus, PD:5¹, PA:1¹, PAE:7¹, BU:6⁻, SL:6¹, CD:1⁺, CDE:13¹, CDMS:4¹; Potamogeton crispus, PD:5⁻, PAE:4⁻, CD:1¹; Potamogeton trichoides, PD:10¹, CD:1¹, CDMS:2¹; Najas minor, PD:5¹, PA:1¹, PAE:4¹, CD:1¹, CDE:4¹; Myriophyllum verticillatum, TL:12⁻, CD:1¹; Potamogeton berchtoldii, CD:1⁺; Trapa natans, PA:1¹, CD:2¹, CDE:6¹; Nymphaea alba, PD:5⁻, 2=1¹, SL:17⁺, 13=2¹; Nymphoides peltata, PA:1⁻, PAE:4¹; Persicaria amphibia, PA:1⁻, PAE:14¹, SL:6⁻; Chara tomentosa, PA:1¹, LM:10¹; Nitella mucronata, PAE:7¹, CD:1⁺, CDE:2⁻, CDMS:2⁻; Nitella hyalina, PD:5⁻, TA:8¹; Agrostis stolonifera, SL:17², CDMS:2¹; Juncus inflexus, SL:6¹, TA:8¹, CDMS:2¹; Ranunculus trichophyllus, PA:1⁺.

Syntaxonomic remarks: Of the four different associations with *Paspalum distichum* described in the western Mediterranean (*Paspalo distichi-Agrostietum verticillatae* Braun-Blanq. 1936; *Ranunculo scelerati-Paspaletum paspalodis* Rivas Goday 1964 corr. Peinado, Bartolomé, Martínez-Parras and Ollala 1988; *Heliotropio supini-Paspaletum paspalodis* Martínez-Parras, Peinado, Bartolomé and Molero 1988; *Paspaletum dilatato-distichi* Herrera and F. Prieto in T.E. Díaz and F. Prieto 1994)

(José et al. 1988; Rivas-Martinez et al. 2001; Neto et al. 2009), we choose to assign our vegetation type as a variant of the first one, which is first in priority order if *P. distichum* dominance stands are treated as a single association. Zotos (2006) identified two communities with *Paspalum distichum* in his study of wet meadows around lakes Trichonida and Lysimachia, including one dominated by *Paspalum distichum*. All the above-mentioned associations and communities have been grouped in the alliance

Paspalo-Agrostion semiverticillati and order Paspalo-Hele-ochloetalia. We do not follow Mucina et al. (2016) who grouped this order of perennial herb-grasslands in the annual-dominated class *Bidentetea* and we prefer the class of perennial plant communities on damp or temporarily flooded, often trampled, disturbed ground, *Plantaginetea majoris*, which Mucina et al. (2016) lumped together with the *Molinio-Arrhenatheretea*.

Class 2. Phragmito-Magnocaricetea

Syntaxon 2.1. *Phragmitetum communis* (Code PA, Table 2, MNT = 1.2)

Appearance and habitat: Extensive and dense (>50% cover) reed beds of *Phragmites australis*, the most commonly noticed and recorded association in most lakes. They cover major parts of the littoral zone, reaching down to 6m depth.

Diagnostic taxa (% constancy): Phragmites australis (100%).

Distribution: Pamvotida, Amvrakia, Kastoria, Lysimachia, Ozeros, Paralimni, Trichonida, Megali Prespa, Mikri Prespa, Volvi, Vegoritida, Zazari, Petres, Doirani and Chimaditida.

Syntaxonomic remarks: This association, widespread across all bioclimatic zones of Eurasia, matches with what has been identified as *Phragmitetum communis* (australis) or Scirpo-Phragmitetum in numerous publications in Greece (Drosos et al. 1996; Sarika-Hatzinikolaou et al. 2003; Grigoriadis et al. 2005; Zotos 2006) and Europe (Preising et al. 1990; Šumberová et al. 2011a; Landucci et al. 2013; Kamberović et al. 2014; Jenačković 2017; Lastrucci et al. 2017).

Syntaxon 2.2. Transitional stands of *Phragmites australis* (Code PAE, Table 2, MNT = 3.4)

Appearance and habitat: Stands of *Phragmites australis* with floristic composition similar to the preceding cluster but with lower *Phragmites* cover (<50%). They are found at the edges of dense reed beds, down to 6m depth, where the *Phragmitetum communis* progressively gives way to, or is interconnected with, aquatic communities such as *Cladophoretum glomeratae*, *Najadetum marinae*, *Lemnetum minoris*, *Ceratophylletum demersi*, *Potamogetono pectinati-Myriophylletum spicati* etc. Due to their sparse cover, other riparian and aquatic plants of the above-mentioned or other plant communities colonize the open areas among and beneath the reeds.

Diagnostic taxa (% constancy): *Phragmites australis* (97%), *Cladophora glomerata* (48.3%), *Najas marina* (17.3%), *Nitellopsis obtusa* (13.8%).

Distribution: Pamvotida, Feneos, Kastoria, Megali Prespa, Volvi, Vegoritida, Zazari, Petres and Chimaditida. Syntaxonomic remarks: This cluster falls within the range of variation of the *Phragmitetum communis*.

Syntaxon 2.3. *Scirpetum lacustris* (Code SL, Table 2, MNT = 5.6)

Appearance and habitat: Dense stands of club-rush *Schoenoplectus lacustris* (>25% cover) and low presence of other helophytes (*Phragmites, Sparganium* and *Typha* spp.). In lacustrine ecosystems, it often forms a zone in mostly shallow waters down to 1m deep, sensitive to wave action, between the open water and the dense reed-bed areas dominated by other species, like *Phragmites australis*.

Diagnostic taxa (% constancy): Schoenoplectus lacustris (100%), Phragmites australis (78%).

Distribution: Volvi, Paralimni, Trichonida, Mikri Prespa, Petres and Chimaditida.

Syntaxonomic remarks: Matches the descriptions of this association (sometimes under the name *Schoenoplectetum lacustris*) from publications in Greece (Sarika-Hatzinikolaou et al. 2003; Dimopoulos et al. 2005; Zotos 2006; Fotiadis et al. 2008) and in Europe (Preising et al. 1990; Lukács et al. 2009; Šumberová et al. 2011a; Landucci et al. 2013; Jenačković 2017).

Syntaxon 2.4. *Typhetum domingensis* (Code TD, Table 2, MNT = 3.1)

Appearance and habitat: Dense stands of the Mediterranean cattail *Typha domingensis* (>25% cover) and low presence of other helophytes (*Phragmites*, *Sparganium*, other *Typha* spp.). *Typha domingensis* stands, like other *Typha* communities, are usually colonizing next to the extensive *Phragmites australis* reed zone, in waters down to 4m deep, under low water fluctuation regime.

Diagnostic taxa (% constancy): Typha domingensis (100%).

Distribution: Trichonida and Chimaditida.

Syntaxonomic remarks: Matches the descriptions of this association in European publications (Biondi and Bagella 2005; Landucci et al. 2013; Jenačković 2017). In Greece, Zotos (2006) recorded two vegetation types in lake Trichonida, one with *Typha domingensis* alone and another with co-dominance of *Phragmites australis*. These are variants of the *Typhetum domingensis*.

Syntaxon 2.5. *Typhetum latifoliae* (Code TL, Table 2, MNT = 2.3)

Appearance and habitat: Dense stands of the cattail *Ty-pha latifolia* (>25% cover) and low presence of other helophytes (*Phragmites*, *Sparganium* and other *Typha* spp.). *Typha latifolia*, like other *Typha* spp., colonizes openings next to the extensive *Phragmites australis* reed zone, in waters down to 2m deep, under low water fluctuation regime.

Diagnostic taxa (% constancy): *Typha latifolia* (100%), *Myriophyllum spicatum* (78%).

Distribution: Pamvotida, Feneos, Vegoritida and Doirani. Syntaxonomic remarks: Matches the descriptions of Greek (Sarika-Hatzinikolaou et al. 2003; Fotiadis et al. 2008) and European publications (Preising et al. 1990; Šumberová et al. 2011a; Landucci et al. 2013; Jenačković 2017). Lower cover of *Typha latifolia* (<25% cover) was recorded in some plots, possibly due to sub-optimal water fluctuation conditions often prevailing in Mediterranean lakes (Coops et al. 2003; Flores and Barone 2005).



Syntaxon 2.6. *Typhetum angustifoliae* (Code TA, Table 2, MNT = 2.1)

Appearance and habitat: Dense stands of the cattail *Typha angustifolia* (>25% cover) and low presence of other helophytes (*Phragmites*, *Sparganium* and other *Typha* spp.). *Typha angustifolia*, like *Typha. latifolia* and *T. domingensis*, forms clonal rhizomatous stands next to *Phragmites australis* reed-beds, in waters to 2m deep, under low water fluctuation regime.

Diagnostic taxa (% constancy): Typha angustifolia (100%).

Distribution: Feneos and Mikri Prespa.

Syntaxonomic remarks: Matches the descriptions from Greek (Sarika-Hatzinikolaou et al. 2003; Dimopoulos et al. 2005, as *Typho-Phragmitetum typhetosum angustifoliae*; Fotiadis et al. 2008) and other European publications (Preising et al. 1990; Šumberová et al. 2011a; Landucci et al. 2013; Jenačković 2017). Lower cover of *Typha angustifolia* (<25% cover) was recorded in some plots which, as in the *Typhetum latifoliae*, may be due to higher than optimal water fluctuation in Mediterranean lakes (Coops et al. 2003; Flores and Barone 2005).

Syntaxon 2.7. *Butometum umbellati* (Code BU, Table 2, MNT = 4.5)

Appearance and habitat: Stands of partly submerged *Butomus umbellatus*, in open water littoral areas, down to 3m deep and with high water-transparency. It is characterized by the helophyte *Butomus umbellatus* (>25% cover) while other helophytes (*Phragmites, Sparganium, Typha*) occur with very low presence. A number of hydrophytes such as *Myriophyllum spicatum* and *Vallisneria spiralis* are constantly filling the gaps between these stands.

Diagnostic taxa (% constancy): Butomus umbellatus (100%), Myriophyllum spicatum (100%).

Distribution: Trichonida.

Syntaxonomic remarks: This association has been identified in various parts of Europe (Preising et al. 1990; Nagy et al. 2009; Šumberová et al. 2011a; Stępień et al. 2015), mostly described from shallower waters than in our study, accompanied by helophytes and lemnids. To our knowledge, a distinct *Butomus umbellatus* community had not been identified before in Greece.

Class 3. Lemnetea

Syntaxon 3.1. *Lemnetum minoris* (Code LM, Table 2, MNT = 5.8)

Appearance and habitat: Mats of the free-floating duckweed *Lemna minor* (>50% cover), accompanied by less abundant lemnids, such as *Spirodela polyrhiza*, *Azolla filiculoides* and other *Lemna* spp., can be found in the littoral zone of still and relatively nutrient-rich freshwater bodies, in very shallow waters 0–1m deep, in spots protected against wave action.

Diagnostic taxa (% constancy): Lemna minor (100%), Azolla filiculoides (73%).

Distribution: Doirani, Vegoritida and Chimaditida.

Syntaxonomic remarks: Matches the descriptions of this widespread association from Greece (Lavrentiades and Pavlidis 1985; Papastergiadou 1990; Zotos 2006) and elsewhere in Europe (Goldyn et al. 2005; Kłosowski and Jabłońska 2009; Šumberová 2011b; Felzines 2012).

Syntaxon 3.2. *Lemno-Utricularietum* and *Utricularietum australis* (Code UV, Table 2, MNT = 5.2)

Appearance and habitat: Open to fully closed submerged carpets of the free-floating carnivorous bladderworts *Utricularia vulgaris* or *Utricularia australis* (>25% cover), with other taxa found in low numbers. As the bladderworts cannot be identified with certainty if not in flower, both species are likely to be included. Frequently present at the surface of the water occur *Hydrocharis morsus-ranae* and lemnids, like *Lemna minor*, *Lemna gibba*, *Spirodela polyrhiza* etc., while *Ceratophyllum demersum* may occur in lower strata of the water column. Vegetation of free-floating bladderworts can be found in very shallow, down to 1m deep, mesotrophic to eutrophic waters protected against wave action.

Diagnostic taxa (% constancy): *Utricularia vulgaris* + *U. australis* (100%).

Distribution: Doirani, Pamvotida, Petres and Chimaditida.

Syntaxonomic remarks: Matches the descriptions of this widespread association from Greece (Sarika-Hatz-inikolaou et al. 2003; Pirini 2011, with *Utricularia vulgaris* and *Chara vulgaris*) and elsewhere in Europe (Šumberová 2011b; Felzines 2012; Džigurski et al. 2016; Cvijanović et al. 2018).

Syntaxon 3.3. *Ceratophylletum demersi* (Code CD, Table 2, MNT = 1.5)

Appearance and habitat: Extensive (>50% cover) carpets of *Ceratophyllum demersum*, a free-floating aquatic macrophyte in variable habitat conditions. Due to its ability to grow well in turbid water, under poor light conditions, it spreads rapidly and may cover the whole water column, possibly limiting the growth of other hydrophytes. While it thrives mostly in shallow waters, it may colonize the full depth range of aquatic macrophytes (in Greece 0–13m).

Diagnostic taxa (% constancy): Ceratophyllum demersum (100%).

Distribution: Amvrakia, Kastoria, Lysimachia, Ozeros, Paralimni, Yliki, Trichonida, Megali Prespa, Mikri Prespa, Volvi, Vegoritida, Petres, Doirani and Chimaditida.

Syntaxonomic remarks: Matches the descriptions in European publications (Goldyn et al. 2005; Šumberová 2011b; Felzines 2012; Lastrucci et al. 2014, 2015; Džigurski et al. 2016; Cvijanović et al. 2018). In Greece, Papastergiadou (1990) and Dimopoulos et al. (2005) identified this association with similar floristic composition, while Sarika-Hatzinikolaou et al. (2003) described a more variable and perhaps composite association, with higher constancies of other *Lemnetea* and *Potamogetonetea* diagnostic taxa (*Lemna minor*, *Spirodela polyrhiza*, *Hydrocharis morsus-ranae*, *Myriophyllum spicatum* and *Potamogeton*

crispus). Gradstein and Smittenberg (1977) recorded a community in which *Ceratophyllum demersum* co-occurs with *Potamogeton trichoides*.

Syntaxon 3.4. Transitional stands of *Ceratophyllum demersum* (Code CDE, Table 2, MNT = 3.5)

Appearance and habitat: Similar to the *Ceratophylletum demersi* but with less cover (<50%) of *Ceratophyllum*, are found at the edges of the dense *Ceratophyllum* stands, in waters down to 13m deep, where the *Ceratophylletum demersi* progressively transitions into other macrophytic communities (*Phragmitetum communis*, *Lemnetum minoris*, *Potamogetono pectinati-Myriophylletum spicati*, *Potametum pectinati* etc.). Other macrophytes like *Phragmites australis*, *Lemna minor*, *Salvinia natans*, *Spirodela polyrhiza*, *Myriophyllum spicatum* and *Stuckenia pectinata* colonize the openings.

Diagnostic taxa (% constancy): Ceratophyllum demersum (100%), Phragmites australis (64%)

Distribution: Volvi, Doirani, Kastoria, Lysimachia, Ozeros, Mikri Prespa, Vegoritida and Chimaditida.

Syntaxonomic remarks: This cluster is a variant of the *Ceratophylletum demersi*.

Syntaxon 3.5. *Ceratophyllum demersum-Myriophyllum spicatum* community (Code CDMS, Table 2, MNT = 2.6)

Appearance and habitat: This cluster represents a transition between *Ceratophylletum demersi* and *Potamogetono pectinati-Myriophylletum spicati* found at the edges of these communities, in waters down to 6m deep, where *Ceratophyllum demersum* becomes sparse and *Myriophyllum spicatum* stands are able to colonize the open spots.

Diagnostic taxa (% constancy): Ceratophyllum demersum (100%), Myriophyllum spicatum (100%).

Distribution: Amvrakia, Paralimni, Yliki, Trichonida, Megali Prespa, Mikri Prespa, Volvi, Vegoritida and Doirani.

Syntaxonomic remarks: These complex stands may be assigned to any of the two associations depending on species' prevalence.

Class 4. Potamogetonetea: Alliance 1. Potamogetonion

Syntaxon 4.(1.)1. *Potamogetono pectinati-Myriophylletum spicati* (Code MS, Table 3, MNT = 2.4)

Appearance and habitat: Dense stands (mostly >50% cover) of the water-milfoil *Myriophyllum spicatum*, a submerged macrophyte with a broad ecological range, common even in disturbed sites. It roots at the lake bottom and reaches the water surface to emerge its inflorescence. These stands colonize waters down to 6m deep, provided water transparency is sufficiently high (chiefly mesotrophic conditions).

Diagnostic taxa (% constancy): Myriophyllum spicatum (100%).

Distribution: Amvrakia, Feneos, Paralimni, Yliki, Trichonida, Megali Prespa, Mikri Prespa, Volvi, Vegoritida, Petres and Doirani.

Syntaxonomic remarks: Matches the descriptions of this association, mostly under the name of *Myriophylle*-

tum spicati, in publications from Greece (Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003; Dimopoulos et al. 2005; Fotiadis et al. 2008; Pirini 2011) and throughout Europe (Goldyn et al. 2005; Klosowski 2006; Šumberová 2011a; Džigurski et al. 2016). One possible reason for occasional lower cover of *Myriophyllum* (<50% cover) may be light limitations in deeper plots (Middelboe and Markager 1997; Klosowski 2006).

Syntaxon 4.(1.)2. *Potamogetonetum pectinati* (Code SP, Table 3, MNT = 1.3)

Appearance and habitat: Dense stands (>50% cover) of *Stuckenia pectinata* (=*Potamogeton pectinatus*), a submerged aquatic plant quite tolerant of brackish and turbid fresh water, found in open water of various depth down to 14m if water transparency permits.

Diagnostic taxa (% constancy): Stuckenia pectinata (100%).

Distribution: Kastoria, Kourna, Trichonida, Volvi, Vegoritida, Petres and Doirani.

Syntaxonomic remarks: Matches the descriptions of this association from Greece (Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003; Pirini 2011) and elsewhere in Europe (Solińska-Górnicka and Symonides 2001; Hrivnák 2002; Melendo et al. 2003; Goldyn et al. 2005; Šumberová 2011a; Lastrucci et al. 2014; Cvijanović et al. 2018).

Syntaxon 4.(1.)3. Transitional stands of *Stuckenia pectina-ta* (Code SPE, Table 3, MNT = 3.6)

Appearance and habitat: Stands of *Stuckenia pectinata*, similar in composition with the preceding cluster, but with lower cover of *Stuckenia* (<50%), were found at the edges of the dense *Stuckenia* stands, in waters down to 4m deep, in contact with other macrophyte communities such as the *Phragmitetum communis*, *Potamogetono pectinati-Myriophylletum spicati* etc., in openings with macrophytes such as *Phragmites australis*, *Myriophyllum spicatum* and *Chara tomentosa*.

Diagnostic taxa (% constancy): Stuckenia pectinata (96%), Phragmites australis (74%).

Distribution: Volvi, Doirani, Kastoria, Kourna, Vegoritida and Petres.

Syntaxonomic remarks: This cluster is a variant of the *Potamogetonetum pectinati*.

Syntaxon 4.(1.)4. *Stuckenia pectinata-Myriophyllum spica-tum* community (Code SPMS, Table 3, MNT = 3.3)

Appearance and habitat: This cluster is transitional between *Potamogetonetum pectinati* and *Potamogetono pectinati-Myriophylletum spicati*, often found at the edges of the two associations, in waters down to 6m.

Diagnostic taxa (% constancy): Stuckenia pectinata (100%), Myriophyllum spicatum (92%).

Distribution: Kastoria, Paralimni, Trichonida, Volvi, Vegoritida and Doirani.

Syntaxonomic remarks: Relevés of this cluster are assignable to any of the two associations depending on species' dominance.



Table 3. Synoptic table of the identified associations and communities belonging to Class *Potamogetonetea*. Taxa constancy in percentage and their average abundance class (r = 0-1%, t = 2-5%, t = 6-20%, t = 21-40, t = 21-40,

Vegetation type code	MS	SP	SPE	SPMS	PP	PCr	PV	PVMS	PL	PLMS	PoN	PCo	PT	NMa	NMaE	NMi	TN	NA	NL	NP	LP
Number of relevés	472	866	41	56	39	5	772	167	116	43	21	6	9	334	80	20	6	7	5	10	34
Mean number of species	2.4	1.3	3.6	3.3	2.2	2.4	2.0	2.8	2.4	3.3	4.7	3.3	6.1	1.8	3.4	6.7	4.3	5.4	1.2	4.8	2.0
POTAMOGETONETEA	۷٠٦	1.5				2.7		2.0	2,7		7.7			1.0	J.+	<u> </u>	7.5	J. T	1+2	0	
Potamogetonion																					
Myriophyllum spicatum	100 ²	4⁺	32¹	92¹	47+	20¹	54 ¹	74 ¹	67¹	981	86¹		45⁺	24⁺	53¹	65¹	50⁺	43¹			
Stuckenia pectinata	10⁺	100³	96¹	100 ²	24 ¹		5 ¹	7÷	1 ¹	3 ¹	5 ¹	67⁺	12¹	13¹	32¹	30¹	34 ^r				
Potamogeton perfoliatus	4+	3⁺	22+	20¹	100 ²		2 ¹	5 ¹				17¹	23 ^r	9 ¹	2O ¹	20⁺	34 ¹				
Potamogeton crispus	1⁺					100¹	1 ¹	2 ¹	2+	3 (r)	5 ¹				3 ¹	15⁺					
Vallisneria spiralis	20 ¹	3 ¹	8 ¹	47¹	3 ¹	20 ¹	100³	100¹	15¹	14⁺	20⁺	50 ¹	23 ^r	5 ¹	20⁺	85¹		43 ¹			
Potamogeton lucens	271			4 ¹			6 ¹	2+	100 ²	87¹	72 ⁺			1 ^r	8¹)	10 ^r	17¹	15¹			
Potamogeton nodosus	10¹						1⁺	2+	19¹	24+	96 ²			1⁺	10¹	20 ¹		15 ^r			
Potamogeton compressus		1 ¹		2 ¹			1 ¹	2 ¹				100³			2 ¹						
Potamogeton trichoides	1 ¹				•				2 ¹	5 ¹	10¹		67¹	1 ¹	2 ¹	5 ¹					
Najas marina	9 ¹	12¹	25⁺	15¹	24+	401	10¹	22 ¹	3 ¹	7+	39⁺	341	12¹	100³	100¹	70¹	17 ^r	58⁺			
Najas minor	3 ¹	1 ^r	3^{r}	6 ^r		40⁺	1 ¹	2^r	3⁺	5⁺	20⁺		12¹	2 ¹	12 ¹	100 ²					
Trapa natans				2 ¹			1⁺	2 ¹		3 ^r		34 ¹				5 ¹	100³			20⁺	
Nymphaeion albae																					
Nymphaea alba	2⁺						1 ¹	1 ¹	1 ¹	3^{r}					2 ¹			100³			
Nuphar lutea																			100³		
Nymphoides peltata																				100 ²	
Ludwigia peploides																					100³
Persicaria amphibia			3 ¹	4 ¹	3 ^r															20 ¹	
Other taxa																					
Phragmites australis	10¹	2 ¹	74 ¹	4⁺	6 ¹		5 ¹	11 ¹	10¹	31¹	24 ¹		23 ¹	7 ¹	28 ²	20 ¹		86⁺		30¹	71¹
Butomus umbellatus	1 ¹	•	•	•	•		3 ¹	1 ¹	•		•					5 ^r	•			30¹	
Schoenoplectus lacustris	1 ¹	•	15¹	•	•		•	1 ¹	•		5 ^r		12¹		2 ¹	10 ^r	•	43⁺		30⁺	
Typha latifolia	•	1+						1 ¹		3 ^r	5 ^r		45¹		2 ¹	5 ^r					
Typha angustifolia	2+										10 ¹							43 ¹			
Eleocharis mitracarpa																				30¹	
Rorippa amphibia								•												30 ^r	
Lemna minor		1 ^r											34⁺		2 ¹	10⁺					3 ¹
Lemna gibba				•	•			•		•			34 ^r		•						
Azolla filiculoides													23 ^r							30⁺	
Spirodela polyrhiza	•	1 ^r						•					34⁺		2 ¹	10⁺	17 ^r			30 ⁻	
Ceratophyllum demersum	30¹	3 ¹	18⁺	8 ¹	8⁺	20 ¹	12¹	35¹	17⁺	4O ¹	24+	34⁺	56⁺	14 ¹	29 ¹	70¹	100 ²	100 ²	20 ^r	30¹	3 ¹
Cladophora glomerata	7 ¹	3 ¹		15¹			7⁺	8⁺			10⁺		56¹	2 ¹	3⁺						3 ¹
Rumex palustris			3^{r}							•			45⁺								
Paspalum distichum	1 ^r	1 ¹	3 ¹	2 ¹					3 ¹	3^{r}	20 ¹		23⁺			30 ¹				•	9 ¹
Chara tomentosa		1 ¹	32 ¹											1 ¹		5 ^r					

Taxa with less than 20% constancy: *Mentha pulegium*, SPMS:2^r; *Samolus valerandi*, SP:1^r; SPE:3^r; *Eleocharis caduca*, SP:1⁺; *Juncus articulatus*, MS:1⁺; *Phyla nodiflora*, PV:1¹, PVMS:1^r; *Ty-pha domingensis*, SPE:5¹, LP:3^r; *Alisma plantago-aquatica*, NP:20⁺; *Lycopus europaeus*, PT:12¹, NP:20^r; *Sparganium erectum*, MNi:5^r, NP:20⁺; *Lythrum salicaria*, NMi:10^r; *Mentha aquatica*, NP:10^r; *Juncus subnodulosus*, PoN:5¹; *Schoenoplectus litoralis*, MS:1¹, SPE:5¹, PV:2¹, PVMS:2⁺, PLMS:3¹; *Salvinia natans*, NMaE:2¹, NMi:15⁺, TN:17¹; *Ceratophyllum submersum*, MS:1¹, SP:1^r; SPE:3¹, SPMS:2^r, PVMS:2¹, NMaE:2^r; *Hydrocharis morsus-ranae*, SP:1¹, NMa:1^r, NMi:15⁺, TN:17¹, NP:10^r; *Utricularia vulgaris*, SP:1^r; *Myriophyllum verticillatum*, PV:1^r; *Potamogeton berchtoldii*, PVMS:3¹, NMi:5¹; *Ranunculus trichophyllus*, MS:1⁺, SP:1⁺, SPMS:2¹, PLMS:3^r, PoN:5^r, TN:17¹, NP:10¹; *Fontinalis antipyretica*, SP:1⁺; *Chara aspera*, SP:1^r, NMa:2¹; *Chara globularis*, PV:1¹; *Chara corfuensis*, SP:4⁺, NMa:1^r, NMaE:5¹; *Nitellopsis obtusa*, MS:1¹, SP:1¹, SPE:5¹, PV:2¹, PVMS:3⁺, NMa:1¹, NMaE:3¹, NMi:10¹; *Chara vulgaris*, MS:1¹, PP:3¹, SPE:8⁺, SPMS:8⁺, PV:1⁺, PVMS:2², NMa:1¹, NMaE:2¹; *Nitella mucronata*, MS:4⁺, SP:1¹, PV:1⁺, PVMS:2¹; *Nitella hyalina*, PoN:5¹, NMi:5¹; *Agrostis stolonifera*, MS:1¹; *Juncus inflexus*, MS:1⁺, PON:10¹, NMaE:2^r; *Scirpoides holoschoenus*, SPMS:2¹, PVMS:1¹, PL:1^r, PLMS:3^r, PON:5^r, NMa:1¹; *Zannichellia pedunculata*, SPE:8², NMa:1⁺.

Syntaxon 4.(1.)5. *Potamogetonetum perfoliati* (Code PP, Table 3, MNT = 2.2)

Appearance and habitat: Submerged stands dominated (>25% cover) by the pondweed *Potamogeton perfoliatus*, accompanied with a lower abundance of *Myriophyllum spicatum*, *Stuckenia pectinata* and *Najas marina*. *Potamogeton perfoliatus* roots at lake bottom and produces emergent inflorescences. It forms extensive stands in waters down to 5m, provided water transparency is high (mostly under mesotrophic conditions).

Diagnostic taxa (% constancy): Potamogeton perfoliatus (100%).

Distribution: Kastoria, Megali Prespa, Volvi, Vegoritida, Zazari and Doirani.

Syntaxonomic remarks: Matches the descriptions from Greek (Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003) and European publications (Solińska-Górnicka and Symonides 2001; Klosowski 2006; Šumberová 2011a).

Syntaxon 4.(1.)6. *Potamogetonetum crispi* (Code PCr, Table 3, MNT = 2.4)

Appearance and habitat: Submerged stands dominated (>25% cover) by *Potamogeton crispus*, accompanied at lower abundance by *Myriophyllum spicatum*, *Vallisneria spiralis* and *Najas marina*. Like *Potamogeton perfoliatus*, *P. crispus* forms extensive stands rooting at lake bottom down to 4m depth under usually meso- to eutrophic conditions.

Diagnostic taxa (% constancy): Potamogeton crispus (100%).

Distribution: Yliki and Megali Prespa.

Syntaxonomic remarks: Matches the descriptions throughout Europe (Hrivnák 2002; Melendo et al. 2003; Goldyn et al. 2005; Šumberová 2011a; Lastrucci et al. 2014, 2015) and Greece (Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003; Grigoriadis et al. 2005).

Syntaxon 4.(1.)7. *Potamogetono-Vallisnerietum spiralis* (Code PV, Table 3, MNT = 2.0)

Appearance and habitat: Dense carpets (>25% cover) of the submerged eel-grass *Vallisneria spiralis* covering the lake-bottom in areas with favourable light and nutrient conditions down to a depth of 10m. Sporadic *Myriophyllum spicatum* and other *Potamogetonetea* taxa root in small openings within the *Vallisneria spiralis* carpet, exploiting the water column above.

Diagnostic taxa (% constancy): Vallisneria spiralis (100%).

Distribution: Amvrakia, Feneos, Kastoria, Ozeros, Paralimni, Yliki, Trichonida, Megali Prespa, Volvi, Vegoritida and Doirani.

Syntaxonomic remarks: Matches the descriptions of this apparently uncommon association scattered in Europe (Gabka 2002; Hutorowicz et al. 2006; Lastrucci et al. 2014) and Greece (Papastergiadou 1990; Grigoriadis et al. 2005; Pirini 2011). A similar association (*Ceratophyllo demersi-Vallisnerietum spiralis*) with higher constancy of *Ceratophyllum demersum* was identified in Serbia (Cvijanović et al. 2018).

Syntaxon 4.(1.)8. *Vallisneria spiralis-Myriophyllum spica-tum* community (Code PVMS, Table 3, MNT = 2.8).

Appearance and habitat: This cluster is transitional between the *Potamogetono-Vallisnerietum* and the *Potamogetono pectinati-Myriophylletum spicati*. If water transparency permits (mostly oligotrophic to mesotrophic conditions) such stands can be found in waters 10m deep.

Diagnostic taxa (% constancy): Vallisneria spiralis (100%), Myriophyllum spicatum (74%).

Distribution: Amvrakia, Feneos, Kastoria, Ozeros, Paralimni, Yliki, Trichonida, Megali Prespa, Volvi, Vegoritida and Doirani.

Syntaxonomic remarks: The relevés can be assigned to either of the two associations depending on species' dominance.

Syntaxon 4.(1.)9. *Potamogetonetum lucentis* (Code PL, Table 3, MNT = 2.4)

Appearance and habitat: Dense stands (>25% cover) of the submerged pondweed *Potamogeton lucens* accompanied at lower abundance by *Myriophyllum spicatum*, *Vallisneria spiralis* and *Potamogeton nodosus*, colonizing waters down to a 6m depth when water transparency permits (usually under oligotrophic to mesotrophic conditions).

Diagnostic taxa (% constancy): Potamogeton lucens (100%).

Distribution: Paralimni and Yliki.

Syntaxonomic remarks: Matches the descriptions in Greece (Gradstein and Smittenberg 1977; Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003; Dimopoulos et al. 2005) and throughout most of Europe (Preising et al. 1990; Hrivnák 2002; Melendo et al. 2003; Goldyn et al. 2005; Klosowski 2006; Šumberová 2011a).

Syntaxon 4.(1.)10. *Potamogeton lucens-Myriophyllum spicatum* community (Code PLMS, Table 3, MNT = 3.3)

Appearance and habitat: This cluster is transitional between *Potamogetono pectinati-Myriophylletum spicati* and *Potamogetonetum lucentis*, characterized by a more or less equivalent constancy and abundance of the two characteristic species (*Myriophyllum spicatum*, *Potamogeton lucens*). It grows in waters down to 6m deep, where *Myriophyllum spicatum* stands become quite sparse and other hydrophytes, mostly *Potamogeton lucens*, occur in openings.

Diagnostic taxa (% constancy): Myriophyllum spicatum (98%), Potamogeton lucens (87%), Phragmites australis (30.3%).

Distribution: Paralimni, Megali Prespa and Mikri Prespa. Syntaxonomic remarks: Relevés of this cluster can be assigned to either of the two associations according to the species' dominance.

Syntaxon 4.(1.)11. *Potamogetonetum denso-nodosi* (Code PoN, Table 3, MNT = 4.7)

Appearance and habitat: Open to fully closed (>25% cover) *Potamogeton nodosus* stands with floating leaves, accompanied at lower abundance by taxa such as *Myrio-phyllum spicatum*, *Potamogeton lucens* and *Najas marina*. *Potamogeton nodosus* forms extensive mats in still freshwater bodies down to 3m deep.

Diagnostic taxa (% constancy): Potamogeton nodosus (96%).

Distribution: Amvrakia, Feneos and Paralimni.

Syntaxonomic remarks: Matches the descriptions of this widespread but infrequent association (Melendo et al. 2003; Šumberová 2011a; Lastrucci et al. 2014; Džigurski et al. 2016; Cvijanović et al. 2018), which in Greece, so far only Papastergiadou (1990, as *Ranunculetum fluitantis* but with similar floristic composition) described in slow-flowing waters.

Syntaxon 4.(1.)12. *Potamogetonetum compressi* (Code PCo, Table 3, MNT = 3.3)

Appearance and habitat: Dense stands (>25% cover) of the submerged pondweed *Potamogeton compressus* accompanied at lower abundance by taxa such as *Vallisneria spiralis*, *Stuckenia pectinata* and *Najas marina*. Its shallow root system is vulnerable to wave action, thus *Potamogeton compressus* forms limited stands in shallow (down to 2m deep) water near lake shorelines.

Diagnostic taxa (% constancy): Potamogeton compressus (100%).

Distribution: Kastoria.

Syntaxonomic remarks: Only a few publications described this association from Eurasia (Kuzmichev et al. 2008;



Borsukevych 2013; Chepinoga et al. 2013), which is rare and/or declining in Europe (Birkinshaw et al. 2013). There are no previous records of this association from Greece.

Syntaxon 4.(1.)13. *Potamogetonetum trichoidis* (Code PT, Table 3, MNT = 6.1)

Appearance and habitat: Dense stands (>25% cover) of the submerged narrow-leaved pondweed *Potamogeton trichoides*, accompanied at lower abundance by taxa such as *Myriophyllum spicatum*, *Ceratophyllum demersum* and *Lemna minor*. Being quite variable, this vegetation type was found in meso-eutrophic waters down to 4m deep, where *Potamogeton trichoides* leaves spaces for a mix of other elodeid and lemnid aquatic macrophytes as well as helophytes.

Diagnostic taxa (% constancy): Potamogeton trichoides (67%), Ceratophyllum demersum (56%), Cladophora glomerata (56%), Myriophyllum spicatum (44.5%), Typha latifolia (44.5%).

Distribution: Kastoria, Lysimachia, Vegoritida, Doirani and Chimaditida.

Syntaxonomic remarks: Similar to the descriptions of Greek (Dimopoulos et al. 2005; Gradstein and Smittenberg 1977; Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003) and European publications (Preising et al. 1990; Hrivnák 2002; Melendo et al. 2003; Šumberová 2011a).

Syntaxon 4.(1.)14. *Najadetum marinae* (Code NMa, Table 3, MNT = 1.8)

Appearance and habitat: Dense submerged carpets (>25% cover) of the naiad *Najas marina* accompanied at lower abundance by *Potamogetonetea* species such as *Potamogeton perfoliatus*, *Myriophyllum spicatum* and *Vallisneria spiralis*. *Najas marina* forms dense carpets on the bottom of still water bodies, down to 5m deep, under mesotrophic to eutrophic and even slightly brackish conditions.

Diagnostic taxa (% constancy): Najas marina (100%).

Distribution: Amvrakia, Kastoria, Kourna, Ozeros, Paralimni, Yliki, Trichonida, Megali Prespa, Mikri Prespa, Volvi, Petres and Doirani.

Syntaxonomic remarks: Described from Europe (Melendo et al. 2003; Šumberová 2011a; Lastrucci et al. 2014; Džigurski et al. 2016; Cvijanović et al. 2018) and Greece (Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003; Pirini 2011).

Syntaxon 4.(1.)15. Transitional stands of *Najas marina* (Code NMaE, Table 3, MNT = 3.4)

Appearance and habitat: Submerged carpets with lower cover (<25%) of *Najas marina* than in the preceding cluster. Found at the edges of dense *Najas marina* stands in waters down to 5m deep where the *Najadetum marinae* progressively gives way to other macrophyte communities such as *Potamogetono pectinati-Myriophylletum spicati*, *Phragmitetum communis*, *Potamogetonetum pectinati* or *Ceratophylletum demersi* etc.). Other macrophytes like *Myriophyllum spicatum*, *Phragmites australis*, *Stuckenia pectinata* and *Ceratophyllum demersum* colonize open *Najas* stands.

Diagnostic taxa (% constancy): Najas marina (100%), Phragmites australis (27.5%).

Distribution: Amvrakia, Kastoria, Kourna, Ozeros, Paralimni, Yliki, Trichonida, Megali Prespa, Mikri Prespa, Volvi, Petres and Doirani.

Syntaxonomic remarks: This cluster is a variant of the *Najadetum marinae*.

Syntaxon 4.(1.)16. *Najadetum minoris* (Code NMi, Table 3, MNT = 6.7)

Appearance and habitat: Dense submerged carpets (>25% cover) of the naiad *Najas minor* sometimes accompanied by *Myriophyllum spicatum*, *Vallisneria spiralis* and *Najas marina*. Both *Najas* species form dense carpets on the bottom of still water bodies, with *N. minor* occurring in more shallow waters down to 3.5m deep, under mesotrophic to eutrophic but not brackish conditions.

Diagnostic taxa (% constancy): Najas minor (100%), Vallisneria spiralis (85%).

Distribution: Kastoria, Paralimni, Megali Prespa and Doirani.

Syntaxonomic remarks: Matches the descriptions throughout Europe (Gabka and Dolata 2010; Šumberová 2011a; Lastrucci et al. 2014). In Greece, only Papastergiadou (1990) gathered a relevé dominated by *Najas minor*, accompanied by *Zannichellia palustris*, which was assigned to the *Zannichellietum palustris*.

Class 4. Potamogetonetea: Alliance 2. Nymphaeion albae

Syntaxon 4.(2.)17. *Trapetum natantis* (Code TN, Table 3, MNT = 4.3)

Appearance and habitat: Open to closed (>25% cover) floating mats of the annual water caltrop *Trapa natans*, most often accompanied by *Ceratophyllum demersum* which tolerates poor light conditions. Nymphaeids such as *Trapa natans* are macrophytes that root at the bottom of still freshwater bodies, but most of their biomass, in particular most of the leaves, is floating on the water surface. *Trapa* occurs in waters down to 3m deep, limiting light levels for other submerged macrophytes underneath.

Diagnostic taxa (% constancy): Trapa natans (100%), Ceratophyllum demersum (100%).

Distribution: Kastoria and Megali Prespa.

Syntaxonomic remarks: The *Trapetum natantis* has been described in Greece, (Lavrentiades and Pavlidis 1985; Papastergiadou 1990) and Europe (Šumberová 2011a; Džigurski et al. 2016; Cvijanović et al. 2018).

Syntaxon 4.(2.)18. *Nymphaeetum albae* (Code NA, Table 3, MNT = 5.4)

Appearance and habitat: Open to closed (>25% cover) floating vegetation mats of the water lily *Nymphaea alba*, most often accompanied by *Ceratophyllum demersum* which is undemanding in terms of light. Like other nymphaeids, *Nymphaea alba* is bottom-rooted and forms dense floating leaf mats, occurring in waters down to 4m deep.

Diagnostic taxa (% constancy): Nymphaea alba (100%), Ceratophyllum demersum (100%), Phragmites australis (86%), Najas marina (57.2%).

Distribution: Paralimni, Trichonida and Mikri Prespa. Syntaxonomic remarks: Similar to the descriptions in Greece (Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003; Zotos 2006) and Europe (Goldyn et al. 2005; Šumberová 2011a; Lastrucci et al. 2014, 2015; Džigurski et al. 2016; Cvijanović et al. 2018).

Syntaxon 4.(2.)19. *Nymphaeo albae-Nupharetum luteae* (Code NL, Table 3, MNT = 1.2)

Appearance and habitat: Open to closed (>25% cover) floating leaf mats of *Nuphar lutea*, rooting at the lake bottom down to 3m deep.

Diagnostic taxa (% constancy): *Nuphar lutea* (100%). Distribution: Pamvotida and Lysimachia.

Syntaxonomic remarks: Matches the descriptions of this association (often under the name of *Myrio-phyllo-Nupharetum luteae*) from Greece (Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003) and from throughout Europe (Preising et al. 1990; Solińska-Górnicka and Symonides 2001; Hrivnák 2002; Melendo et al. 2003; Goldyn et al. 2005; Gabka and Dolata 2010; Šumberová 2011a; Lastrucci et al. 2015; Džigurski et al. 2016; Cvijanović et al. 2018).

Syntaxon 4.(2.)20. *Nymphoidetum peltatae* (Code NP, Table 3, MNT = 4.8)

Appearance and habitat: Open to closed (>25% cover) floating mats of *Nymphoides peltata* accompanied by low-abundant lemnids and helophytes. Like all other nymphaeids, *Nymphoides peltata* forms a dense floating leaf canopy, bottom-rooted in shallow waters down to 2m deep, sharing its space with other floating or emerged macrophytes.

Diagnostic taxa (% constancy): Nymphoides peltata (100%).

Distribution: Pamvotida and Megali Prespa.

Syntaxonomic remarks: Similar to the descriptions in Greece (Lavrentiades and Pavlidis 1985, co-dominating with *Trapa natans*; Papastergiadou 1990; Sarika-Hatzinikolaou et al. 2003) and Europe (Preising et al. 1990; Gabka and Dolata 2010; Šumberová 2011a; Lastrucci et al. 2014; Džigurski et al. 2016; Cvijanović et al. 2018).

Syntaxon 4.(2.)21. *Ludwigia peploides* community (Code LP, Table 3, MNT = 2.0)

Appearance and habitat: Open to closed (>25% cover) mats of *Ludwigia peploides* subsp. *montevidensis*, an amphibious perennial macrophyte forming creeping mats on the wet mud and flooded shores of freshwater bodies or floating mats on the muddy surface of the riparian zone. The floating mats, often found within the gaps of *Phragmites australis* reedbeds, reach down to 2m deep, leaving no room for other aquatic macrophytes.

Diagnostic taxa (% constancy): *Ludwigia peploides* ssp. *montevidensis* (100%).

Distribution: Lysimachia.

Syntaxonomic remarks: Ludwigia peploides subsp. montevidensis, native to South America, is locally naturalized in South Europe, SW Asia and other continents where it is often invasive (Dutartre 1986; Zotos et al. 2006). In South America the association *Polygono-Ludwigietum peploidis* has been described (Padovani et al. 1993; Hauenstein et al. 2002), where Ludwigia peploides is often (but not always) accompanied by Persicaria hydropiperoides which does not occur in Europe. We did not find Ludwigia peploides relevés from Europe other than those published by Zotos (2006) and Zotos et al. (2006), together with Paspalum distichum or dominated by Phragmites australis. We found Ludwigia peploides as the dominant species associated with *Phragmites*. Taking into consideration the ecological similarities between Ludwigia peploides and Ludwigia grandiflora (Zotos et al. 2006), a diagnostic taxon of the Nymphaeion, we assign with some reservations the *Ludwigia peploides* community to that alliance.

Class 5. Platyhypnidio-Fontinalietea antipyreticae

Syntaxon 5.1. Fontinalietum antipyreticae (Code FA, Table 4, MNT = 4.0)

Appearance and habitat: Patchy carpets dominated by the water moss *Fontinalis antipyretica* usually developing under shady conditions, on rocks in very shallow water (down to 0.5m deep), often in very clear (oligo-mesotrophic) streams, sometimes in lacustrine littoral zones.

Diagnostic taxa (% constancy): Fontinalis antipyretica (100%).

Distribution: Kourna and Feneos.

Syntaxonomic remarks: Matches the descriptions from Europe (Dawson and Szoszkiewicz 1999; *Pedrotti* 2008; Ceschin et al. 2010; Grzybowski et al. 2010). In Greece, only Gradstein and Smittenberg (1977) published a relevé of *Fontinalis antipyretica* together with *Stuckenia pectinata*.

Class 6. Charetea intermediae

Syntaxon 6.1. Charetum globularis (Code ChG, Table 4, MNT = 1.4)

Appearance and habitat: Dense (>25% cover) underwater stonewort meadows of *Chara globularis* tolerating a broad range of ecological conditions but thriving in oligo-mesotrophic calcareous freshwater lakes to a depth of 8m.

Diagnostic taxa (% constancy): Chara globula-ris (100%).

Distribution: Feneos.

Syntaxonomic remarks: Matches the descriptions of this association from publications in Europe (Šumberová et al. 2011b; Iakushenko and Borysova 2012; Azzella et al. 2013). In Greece, to our knowledge, no distinct *Chara globularis* community has been hitherto identified.

Syntaxon 6.2. *Magno-Charetum hispidae* (Code CH, Table 4, MNT = 2.1)

Appearance and habitat: Sparse underwater stonewort meadows dominated by *Chara corfuensis* (= *Chara hispida*



Table 4. Synoptic table of the identified associations and communities belonging to Classes *Platyhypnidio-Fontinalietea* antipyreticae, Charetea intermediae and Stigeoclonietea tenuis. Taxa constancy in percentage and their average abundance class (r = 0.1%, t = 2.5%, t = 6.20%, t = 21.40, t = 41.60%, t = 61.80%, t = 81.100%) superscripted are shown. Companion taxa with less than 20% constancy are shown at the end of the Table. Diagnostic taxa for each vegetation type are marked in bold (see relevant text and Table 5 for vegetation type codes).

Vegetation type code	FA	ChG	СН	CHE	NO	CV	CA	ΝΜυ	NHy	CIGL	CIGM
Number of relevés	4	105	32	10	51	139	11	26	6	83	35
Mean number of species	4.0	1.4	2.1	4.9	1.8	1.1	1.1	2.1	5.3	2.3	3.3
PLATYHYPNIDIO-FONTINALIETEA ANT	TIPYRETICAE										
Fontinalis antipyretica	100¹	•	7⁺	10 ^r		•					
CHARETEA INTERMEDIAE											
Chara globularis	50 ¹	100³				3 ¹			50⁺		
Chara corfuensis			100¹	100¹							
Nitellopsis obtusa					100³	•					
Chara tomentosa					2O ¹						6 ¹
Chara vulgaris		1 ¹			4 ¹	100 ²			17¹		
Chara aspera	25 ^r					2⁺	100++	•			
Nitella mucronata					•	•	•	100 ²		4+	
Nitella hyalina		2 ¹			•	1 ¹	•	•	1004		
STIGEOCLONIETEA TENUIS											
Cladophora glomerata	•	•	4 ¹	20 ^r	•		•	12+	•	100 ²	100 ²
Other taxa											
Eleocharis caduca			10⁺	90 ²	•						
Paspalum dilatatum	25 ¹	•	4 ^r	70 ¹	•	2 ²					•
Elatine alsinastrum	25 ^r		4 ^r	70¹	•	1 r					
Samolus valerandi	25 ^r			20 ^r		2^r					
Phragmites australis	•	•			61	•		8⁺	50¹	16 ¹	4O ¹
Typha latifolia	25 ¹	4 ¹							841	5 ¹	
Typha angustifolia	50⁺	61				•			841		
Eleocharis palustris	50 ¹	1 ¹	•		•	•		•		•	
Myriophyllum spicatum	25 ¹	12¹	•		2 ¹	1 ^r		24 ¹	34 ^r	17 ¹	83 ²
Stuckenia pectinata	•	1 ¹	75¹	70⁺	201	1 ¹	10 ^r	27 ¹		19⁺	46 ¹
Vallisneria spiralis	•	6+						8+	50⁺	21 ¹	6+
Ceratophyllum demersum		1 ^r			6 ¹		•	31⁺		16¹	32 ¹

Taxa with less than 20% constancy: Rumex palustris, CGl:4⁺; Paspalum distichum, CGl:8⁺; Typha domingensis, NO:4²; Mentha aquatica, CGm:6¹; Mentha pulegium, CG:1¹, NHy:17^r; Schoenoplectus lacustris, NHy:17^r, CGm:3¹; Juncus inflexus, NHy:17^r; Lemna minor, CGl:4⁺; Azolla filiculoides, CGl:3⁺; Ceratophyllum submersum, NMu:4¹, CGl:2^r; Potamogeton perfoliatus, NO:2¹, CGl:4¹, CGm:3¹; Potamogeton lucens, CGl:2¹; Potamogeton nodosus, CGl:2^r; Najas marina, CG:7⁺, NO:14¹, CGl:8¹, CGm:3¹; Najas minor, CGl:2^r; Trapa natans, NO:2¹; Zannichellia pedunculata, CH:4^r, CV:2¹; Ranunculus trichophyllus, CGl:3⁺; Nitella gracilis, CG:4¹.

f. *corfuensis*, Wood 1962) in oligo-mesotrophic calcareous waters, down to 3m deep.

Diagnostic taxa (% constancy): *Chara corfuensis* (100%). Distribution: Kourna (found also by Langangen 2012).

Syntaxonomic remarks: Matches the descriptions of this association (often under the name *Charetum hispidae*) from Europe (Preising et al. 1990; Hrivnák et al. 2005; Pelechaty and Pukacz 2006; Šumberová et al. 2011b). Pirini (2011) lumped relevés from lake Vegoritida containing *Bolboschoenus maritimus* and *Chara hispida* in a complex community.

Syntaxon 6.3. Transitional stands of *Chara corfuensis* (Code CHE, Table 4, MNT = 4.9)

Appearance and habitat: *Chara corfuensis* stands similar in composition to the previous (CH), but with lower stonewort cover (<10%), were found at the shallow edges of the littoral zone, in 0–0.5m deep waters, where the *Magno-Charetum hispidae* merges into a community dominated by *Eleocharis caduca* and other helophytes.

Diagnostic taxa (% constancy): Chara corfuensis (100%), Eleocharis caduca (70%), Paspalum dilatatum (70%).

Distribution: Kourna.

Syntaxonomic remarks: This cluster is a variant of the *Magno-Charetum hispidae*.

Syntaxon 6.4. *Nitellopsidetum obtusae* (Code NO, Table 4, MNT = 1.8)

Appearance and habitat: Sparse to dense (25% cover) underwater stonewort meadows dominated by *Nitellopsis obtusa* occurring from oligotrophic to meso-eutrophic calcareous deep standing waters down to 12m deep with muddy deposits.

Diagnostic taxa (% constancy): Nitellopsis obtusa (100%).

Distribution: Feneos, Kastoria and Petres.

Syntaxonomic remarks: Matches the descriptions in publications of this association scattered in Europe (Solińska-Górnicka and Symonides 2001; Iakushenko and Borysova 2012; Kipriyanova 2013). In Greece, a distinct *Nitellopsis obtusa* community has not yet been identified.

Syntaxon 6.5. *Charetum vulgaris* (Code CV, Table 4, MNT = 1.1)

Appearance and habitat: Sparse to dense (>25% cover) underwater stonewort meadows dominated by *Chara vulgaris* in oligo-mesotrophic neutral to slightly alkaline standing fresh water, down to 6m deep.

Diagnostic taxa (% constancy): *Chara vulgaris* (100%). Distribution: Feneos and Kourna.

Table 5. Syntaxonomic overview of the plant associations and communities found in the current study.

Plantaginetea majoris Tx. et Preising ex von Rochow 1951

Paspalo-Heleochloetalia Br.-Bl. ex Rivas Goday 1956 Paspalo-Agrostion semiverticillati Br.-Bl. in Br.-Bl. et al. 1952

(PhN) Phyla nodiflora community

(PD) Paspalo distichi-Agrostietum verticillatae Br.-Bl. in Br.-Bl et al. 1936

Phragmito-Magnocaricetea Klika in Klika et Novák 1941

Phragmitetalia Koch 1926

Phragmition communis Koch 1926

(PA) Phragmitetum communis Savič 1926

(PAE) Phragmites australis transitional community

(SL) Scirpetum lacustris Chouard 1924

(TD) Typhetum domingensis Brullo et al. 1994

(TL) Typhetum latifoliae Nowiński 1930

(TA) Typhetum angustifoliae Pignatti 1953

Oenanthetalia aquaticae Hejný ex Balátová-Tuláčková et al. 1993

Eleocharito palustris-Sagittarion sagittifoliae Passarge 1964

(BU) Butometum umbellati Philippi 1973

Lemnetea O. de Bolòs et Masclans 1955

Lemnetalia minoris O. de Bolòs et Masclans 1955

Lemnion minoris O. de Bolòs et Masclans 1955

(LM) Lemnetum minoris von Soó 1927

Utricularion vulgaris Passarge 1964

(UV) Lemno-Utricularietum vulgaris Soó 1947 + Utricularietum australis Müller et Görs 1960

Stratiotion Den Hartog et Segal 1964

(CD) Ceratophylletum demersi Corillion 1957

(CDE) Ceratophyllum demersum transitional community

(CDMS) Ceratophyllum demersum – Myriophyllum spicatum mixed community

Potamogetonetea Klika in Klika et Novák 1941

Potamogetonetalia Koch 1926

Potamogetonion Libbert 1931

(MS) Potamogetono pectinati-Myriophylletum spicati Rivas-Goday 1964

(SP) Potamogetonetum pectinati Carstensen ex Hilbig 1971

(SPE) Stuckenia pectinata transitional community

(SPMS) Stuckenia pectinata – Myriophyllum spicatum mixed community

(PP) Potamogetonetum perfoliati Miljan 1933

(PCr) Potamogetonetum crispi von Soó 1927

(PV) Potamogetono-Vallisnerietum spiralis Braun-Blanquet 1931

(PVMS) Vallisneria spiralis – Myriophyllum spicatum mixed community

(PL) Potamogetonetum lucentis Hueck 1931

(PLMS) Potamogeton lucens - Myriophyllum spicatum mixed community

(PoN) Potamogetonetum denso-nodosi de Bolós 1957

(PCo) Potamogetonetum compressi Tomaszewicz 1979

(PT) Potamogetonetum trichoidis Tüxen 1974 (Nma) Najadetum marinae Fukarek 1961

(NMaE) Najas marina transitional community

(NMi) Najadetum minoris Ubrizsy 1961

Nymphaeion albae Oberd. 1957

(TN) Trapetum natantis Kárpáti 1963

(NA) Nymphaeetum albae Vollmar 1947

(NL) Nymphaeo albae-Nupharetum luteae Nowiński 1927

(NP) Nymphoidetum peltatae Bellot 1951

(LP) Ludwigia peploides community

Platyhypnidio-Fontinalietea antipyreticae Philippi 1956

Leptodictyetalia riparii Philippi 1956

Fontinalion antipyreticae W. Koch 1936

(FA) Fontinalietum antipyreticae Kaiser 1926

Charetea intermediae F. Fukarek 1961

Charetalia intermediae Sauer 1937

Charion intermediae Sauer 1937

(CG) Charetum globularis Corillion 1949

(CH) Magno-Charetum hispidae Corillion 1957

(CHE) Chara corfuensis transitional community (NO) Nitellopsidetum obtusae Dambska 1961

Charion vulgaris (W. Krause et Lang 1977) W. Krause 1981

(CV) Charetum vulgaris Corillion 1949

(CA) Charetum asperae Corillion 1957

Nitelletalia W. Krause 1969

Nitellion syncarpo-tenuissimae W. Krause 1969

(NMu) Nitelletum mucronatae Tomaszewicz ex Hrivnák et al. 2001

(NHy) Nitelletum hyalinae Corillion 1949

Stigeoclonietea tenuis Arendt 1982

Stigeoclonietalia tenuis Arendt 1982 Cladophorion fractae Margalef 1951

(CGI) Cladophoretum glomeratae Sauer 1937, lake substratum variant (CGm) Cladophoretum glomeratae Sauer 1937, macrophyte-substratum

Syntaxonomic remarks: Matches the descriptions of this widespread association from Greece (Grigoriadis et al. 2005; Pirini 2011, with Utricularia vulgaris) and elsewhere in Europe (Preising et al. 1990; Goldyn et al. 2005; Hrivnák et al. 2005; Pelechaty and Pukacz 2006; Šumberová et al. 2011b; Iakushenko and Borysova 2012; Kipriyanova 2013).

Syntaxon 6.6. *Charetum asperae* (Code CA, Table 4, MNT = 1.1)

Appearance and habitat: Patchy and monospecific underwater stonewort meadows of Chara aspera, growing in calcareous oligo-mesotrophic still water, on substrate with gravel or sand near the shoreline, down to 2m deep.

Diagnostic taxa (% constancy): Chara aspera (100%).

Distribution: Kourna.

Syntaxonomic remarks: Matches the descriptions of this association from elsewhere in Europe (Heuff 1984; Preising et al. 1990; Solińska-Górnicka and Symonides 2001; Pelechaty and Pukacz 2006; Iakushenko and Borysova 2012; Azzella et al. 2013; Kipriyanova 2013). In Greece, no distinct Chara aspera community has yet been identified.

Syntaxon 6.7. *Nitelletum mucronatae* (Code NMu, Table 4, MNT = 2.1)

Appearance and habitat: Sparse to dense (>25% cover) underwater stonewort meadows of Nitella mucronata found in water depths between 3 and 7m, in meso-eutrophic more or less alkaline freshwater.

Diagnostic taxa (% constancy): Nitella mucronata (100%).

Distribution: Vegoritida.

Syntaxonomic remarks: Matches the descriptions of this association in Europe (Hrivnák 2002; Iakushenko and Borysova 2012; Täuscher and van de Weyer 2015). In Greece, a community dominated by *Nitella mucronata* has not yet been identified.

Syntaxon 6.8. Nitelletum hyalinae (Code NHy, Table 4, MNT = 5.3)

Appearance and habitat: Sparse to dense (>25% cover) underwater stonewort meadows of Nitella hyalina in very shallow clear oligotrophic alkaline waters, 0–1m deep.

Diagnostic taxa (% constancy): Nitella hyalina (100%). Distribution: Feneos.

Syntaxonomic remarks: Matches the descriptions of this association from Europe (Golub et al. 1991; Landucci et al. 2011; Csiky et al. 2014). In Greece, no community dominated by *Nitella hyalina* has been identified yet.

Class 7. Stigeoclonietea tenuis

Syntaxon 7.1. Cladophoretum glomeratae, lake-substratum variant (Code ClGL, Table 4, MNT = 2.3)

Appearance and habitat: Open to closed (>25% cover) submerged carpets of the filamentous macroalgae Clado-



phora glomerata, found in stagnant eutrophic lowland waters. It is a quite light-demanding taxon which is often entangled with other macrophytes (subsequent cluster), or attached to the rocky substrate. These relevés, with a low cover of other aquatic macrophytes, were found in waters down to 5m deep.

Diagnostic taxa (% constancy): Cladophora glomerata (100%).

Distribution: Amvrakia, Paralimni, Trichonida, Megali Prespa and Vegoritida.

Syntaxonomic remarks: Matches the descriptions of this association from Europe (Margalef 1949; Den Hartog 1959; Carretero 1986). In Greece, *Cladophoretum glomeratae* has not yet been identified.

Syntaxon 7.2. *Cladophoretum glomeratae*, macrophyte-substratum variant (Code ClGM, Table 4, MNT = 3.3)

Appearance and habitat: This cluster is also assigned to the *Cladophoretum glomeratae* defined by the dominance of the benthic filamentous macroalgae *Cladophora glomerata*, but in this cluster it is accompanied by other aquatic macrophytes, especially *Myriophyllum spicatum* and *Stuckenia pectinata*, serving as the algae's substrate. The relevés within this cluster have been recorded in waters down to 4m deep.

Diagnostic taxa (% constancy): Cladophora glomerata (100%), Myriophyllum spicatum (82.9%).

Distribution: Kourna, Vegoritida and Petres. Syntaxonomic remarks: See preceding unit.

Relation of phytosociological units to environmental parameters

Water depth is widely known to be an important environmental parameter which affects the distribution of aquatic plants, by regulating prevailing light conditions, temperature, water chemistry, wave action and substrate granulometry (Spence and Chrystal 1970; Chambers and Kaiff 1985; Middelboe and Markager 1997). Each macrophyte species has its own water depth tolerance limits, which depend on its morphological and physiological characteristics. However, due to the competition for space, light and nutrients from other macrophyte species they are not free to colonize the water volume that falls within their tolerance limits (McCreary 1991; Gopal and Goel 1993; Gross 2003). These mechanisms produce distinct zonation patterns in aquatic vegetation along water depth gradients (Spence 1982; Shipley et al. 1991). Figure 2 summarizes the depth distribution of the 46 described vegetation types, as recorded in the lakes that were surveyed in the current study. Among the helophytic vegetation types (Plantaginetea majoris; Phragmito-Magnocaricetea) the Phyla nodiflora community, and the Paspalo distichi-Agrostietum verticillatae, Scirpetum lacustris, and Typhetum angustifoliae were recorded colonizing the littoral zones to a depth of 1.5m. The *Typhe*tum domingensis, Typhetum latifoliae, and Butometum umbellati were able to reach a bit deeper down to a depth of 2m, while the Phragmitetum communis which dominates the littoral zone of Greek lakes, quite often reach-

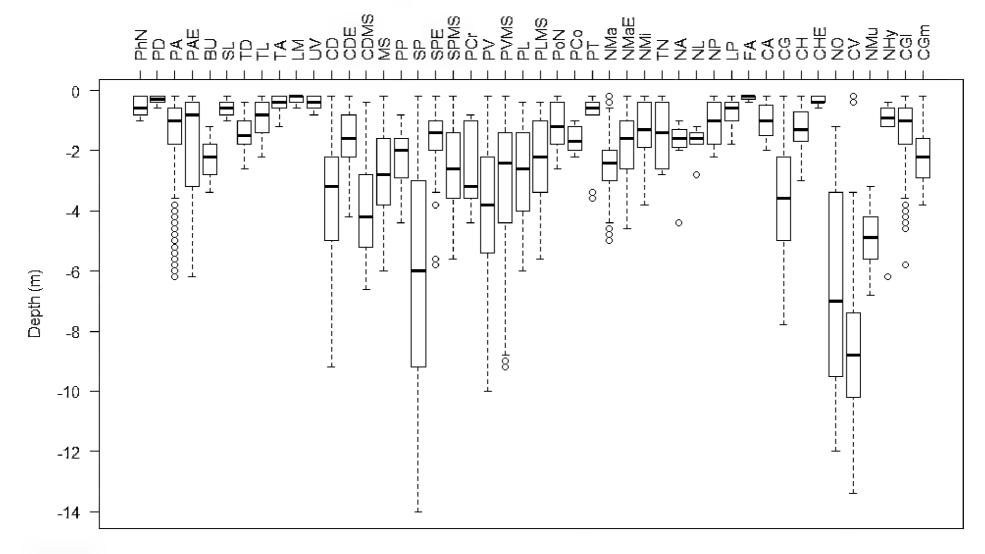


Figure 2. Depth distribution of the 46 described associations and communities (see related text and Table 5 for vegetation type abbreviations). Bold lines represent median values and boxplots represent the interquartile range (IQR) between first and third quartiles (25% and 75%). Whiskers represent minimum and maximum values excluding outlier values (symbolized by an empty circle), which are calculated as values beyond the range of 1.5xIQR.

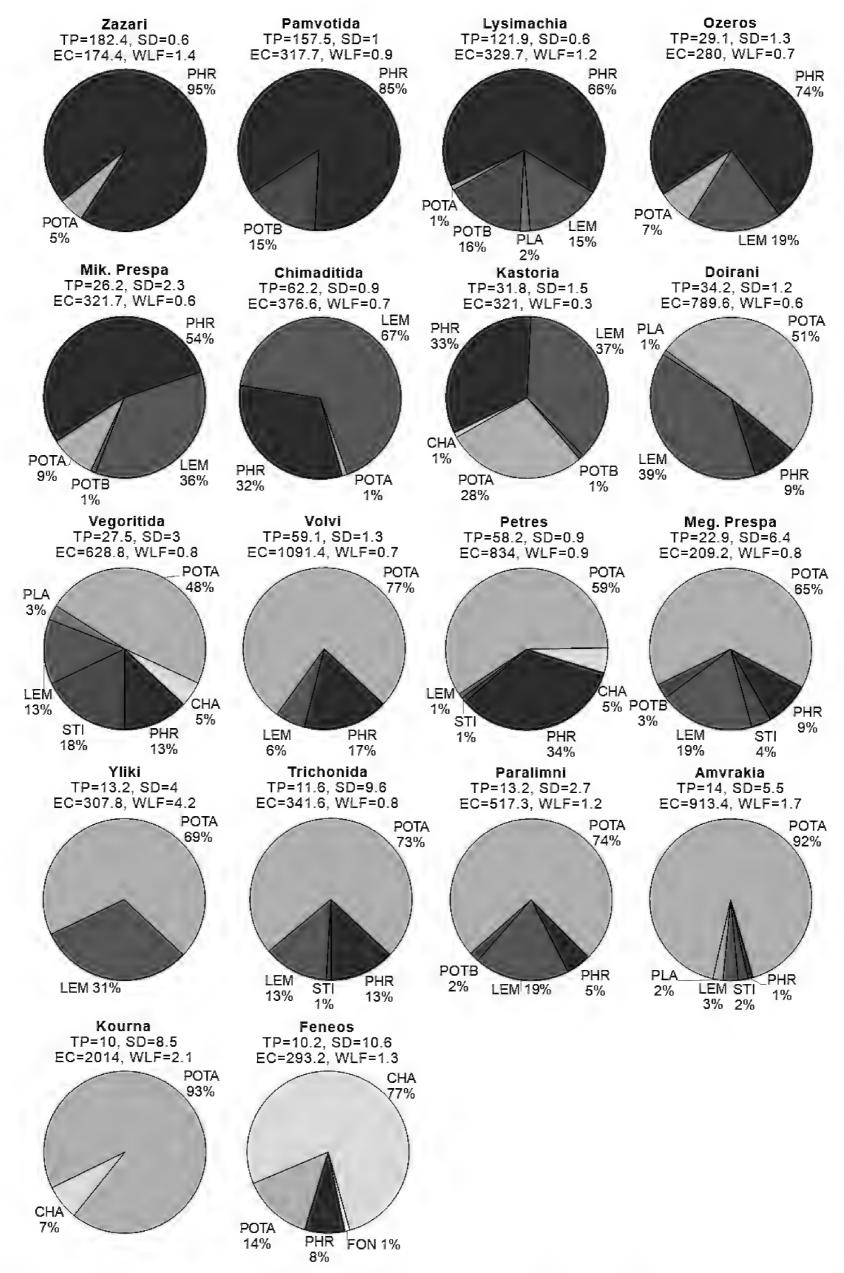


Figure 3. Distribution of higher-rank syntaxa (classes to alliances) in the lakes of the current study (number of relevés per syntaxon to total number or relevés in each lake). PLA: Plantaginetea majoris; PHR: Phragmito-Magnocaricetea; LEM: Lemnetea; POTA: Potamogetonion; POTB Nymphaeion albae; FON: Platyhypnidio-Fontinalietea antipyreticae; CHA: Charetea intermediae; STI: Stigeoclonietea tenuis. Environmental data [TP: Annual mean total phosphorus (μg/L); SD: Secchi depth transparency in meters; EC: Electrical conductivity (μS/cm); WLF: Annual water level fluctuation in meters] are also presented.



Table 6. Overview of the relationships between the abundance of higher-rank syntaxa (classes to alliances) for each lake within the current study and its environmental variables. Pearson's correlation coefficient (*R*) and the p-value of significance are given for each linear regression. Significant relationships (*p* < 0.05) are marked in bold. The two final rows of the table contain part of the results of the multiple linear regression analysis with the involvement of more than one higher-rank syntaxa (one with all the higher-rank syntaxa and one with those giving the best solution for all the environmental parameters). PLA: *Plantaginetea majoris*; PHR: *Phragmito-Magnocaricetea*; LEM: *Lemnetea*; POTA: *Potamogetonion*; POTB *Nymphaeion albae*; FON: *Platyhypnidio-Fontinalietea antipyreticae*; CHA: *Charetea intermediae*; STI: *Stigeoclonietea tenuis*; TP: Annual mean total phosphorus (μg/L); SD: Secchi depth transparency in meters; EC: Electrical conductivity (μS/cm); WLF: Annual water level fluctuation in meters.

Syntaxa in regression	Т	Р	S	D	E	С	WLF	
	R	р	R	р	R	р	R	р
PHR	0.821	<0.001	-0.585	0.011	-0.444	0.065	-0.296	0.233
STI	-0.158	0.532	0.049	0.846	0.019	0.940	-0.118	0.641
LEM	-0.221	0.379	-0.321	0.194	-0.299	0.228	-0.131	0.604
PLA	-0.006	0.981	-0.099	0.695	0.098	0.699	-0.036	0.888
POTA	-0.584	0.011	0.441	0.067	0.630	0.005	0.341	0.166
POTB	0.594	0.009	-0.282	0.258	-0.235	0.348	-0.078	0.759
CHA	-0.210	0.402	0.567	0.014	-0.064	0.802	0.050	0.845
FON	-0.187	0.458	0.545	0.019	-0.147	0.560	0.040	0.876
PHR+STI+LEM+PLA+POTA+POTB+CHA+FON	0.860	0.026	0.802	0.091	0.893	0.009	0.410	0.953
PHR+POTA+POTB+CHA+FON	0.858	0.003	0.788	0.024	0.813	0.013	0.375	0.844

es down to a depth of 4m. Freely floating macrophytes (Lemnetea) and anchored floating macrophytes (Nymphaeion albae) are also restricted to shallow waters down to 1m and 3m deep respectively, with the exception of the Ceratophylletum demersi which can be found commonly down to 6m deep. Submerged hydrophytes (Potamogetonion; Charetea intermediae) predominantly colonize the deeper part of the euphotic zone of lacustrine littoral areas, between the zone colonized by emergent vegetation and the aphotic zone. Therefore, the majority of vegetation types belonging to Potamogetonion or Charetea intermediae are usually located in a depth zone starting at 1-2m and reaching 4-6m deep (in Greek waters), depending on the variability of light penetration and the specific lake physico-chemical characteristics. In cases where the euphotic zone reaches more than 6-8m deep, the Potamogetonetum pectinati, Nitellopsidetum obtusae, and Charetum vulgaris are the most commonly found vegetation types.

An equally important environmental parameter to water depth, that influences the distribution of aquatic plants, is prevailing light conditions. Light penetration in lacustrine ecosystems is highly dependent upon their water quality status (Phillips et al. 1978; Canfield et al. 1985; Middelboe and Markager 1997). Nutrient loading and eutrophication lead to the growth of phytoplankton, epiphytes and filamentous algae, which leads to increased shading and light attenuation. As a result, macrophyte dominance is reduced due to their biomass decline, plant cover reduction and loss of species richness (Phillips et al. 1978; 2016; Sand-Jensen 2000). Figure 3 and Table 6 summarize the relationships we found between the distribution and abundance of higher-rank syntaxa for each lake and the prevailing physico-chemical and hydrological conditions. Positive and significant correlations were found between the distribution of Phragmito-Magnocaricetea and Nymphaeion albae with total phosphorus concentrations, while Potamogetonion was negatively

correlated. In addition, positive and significant correlations were found between Charetea intermediae and Platyhypnidio-Fontinalietea antipyreticae with Secchi depth transparency, while Phragmito-Magnocaricetea was negatively correlated. Only *Potamogetonion* was positively correlated with electrical conductivity. No syntaxon was correlated significantly with water level fluctuation. Multiple linear regression analysis produced the best solution for the above-mentioned environmental parameters (TP, SD and EC) using the combination of distribution values for five syntaxa: Phragmito-Magnocaricetea, Potamogetonion, Nymphaeion albae, Charetea intermediae, and *Platyhypnidio-Fontinalietea*. The distribution patterns of these five higher-rank syntaxa appear to act as good indicators of lake eutrophication. Raised total phosphorus concentrations in lake water and lowered water transparency led to the dominance of *Phragmito-Magnocaricetea*, and Nymphaeion albae syntaxa in aquatic vegetation. The expansion of Potamogetonion, Charetea intermediae, and Platyhypnidio-Fontinalietea syntaxa in aquatic vegetation is associated with lower total phosphorus concentrations and higher values of water transparency.

These results are of relevance for WFD assessment purposes and are similar to those presented in Poikane et al. (2018) that reviewed national macrophyte-based approaches for assessing ecological status according to the WFD. Poikane et al. (2018) reported that a marked decline in submerged vegetation, especially Charophyta (characterizing 'good' status according to WFD), and an increase in abundance of floating and emerged plants (characterizing 'less than good' status) were the most significant changes along the ecological status gradient. Similar results have also been reported from other areas within Europe, where the indicator value of different groups of taxa belonging to these syntaxa were tested against eutrophication levels in the context of WFD assessement systems (e.g. Penning et al. 2008a, 2008b; Søndergaard et al. 2010; Kolada 2016).

Conclusions

The current study is a national-scale phytosociological survey of freshwater lake vegetation, based on the most recent data available (years 2013–2016). Forty-six vegetation types were identified and interpreted for eighteen major Greek freshwater lakes. Among these vegetation types, the following are new records for Greece: Phyla nodiflora community, Butometum umbellati, Potamogetonetum denso-nodosi, Potamogetonetum compressi, Najadetum minoris, Fontinaletum antipyreticae, Charetum globularis, Magno-Charetum hispidae, Nitellopsidetum obtusae, Charetum asperae, Nitelletum mucronatae, Nitelletum hyalinae, *Cladophoretum glomeratae*. A primary analysis on the distribution of higher-rank syntaxa of the 46 vegetation types showed that the majority of these types are significantly affected by physico-chemical parameters indicative of higher levels of eutrophication. Aquatic plant communities could be utilized in eutrophication indices to broaden the assessment of the ecological status of freshwater lakes. Additional research on this topic is needed.

Data availability

The data that support the findings of this study were used under license from The Goulandris Natural History Museum, Greek Biotope/Wetland Centre (EKBY). They are available from the lead author upon reasonable request and with permission of The Goulandris Natural History Museum, Greek Biotope/Wetland Centre (EKBY).

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Author contributions

D.Z. and I.T. conceived of the research idea; D.Z. collected vegetation data; V.T. supervised environmental parameters samplings and analyses; D.Z. and I.T. performed statistical analyses; E.B. supervised vegetation type descriptions and syntaxonomical decisions; D.Z., with contributions from I.T. and E.B., wrote the paper; all authors discussed the results and commented on the manuscript.

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E-mail and ORCID

Dimitrios Zervas (Corresponding author, dzervas@ekby.gr), ORCID: https://orcid.org/0000-0002-2892-6046 Ioannis Tsiripidis (tsiripid@bio.auth.gr)
Erwin Bergmeier (erwin.bergmeier@bio.uni-goettingen.de)
Vasiliki Tsiaoussi (vasso@ekby.gr)

Supplementary material

Supplementary material 1

Bibliographic data sources of Greek aquatic plant communities.

Link: https://10.3897/VCS/2020/48377.suppl1

Supplementary material 2 Summary of the recorded taxa in the studied lakes. Link: https://doi.org/10.3897/VCS/2020/48377.suppl2

Supplementary material 3 Resulting graphs of cluster statistics.

Link: https://doi.org/10.3897/VCS/2020/48377.suppl3

Supplementary material 4 Classification dendrogram of the current study.

Link: https://doi.org/10.3897/VCS/2020/48377.suppl4



Supplementary material 5 Selected taxa combinations of diagnostic taxa.

Link: https://doi.org/10.3897/VCS/2020/48377.suppl5

Supplementary material 6
Distribution of the recorded vegetation types.

Link: https://doi.org/10.3897/VCS/2020/48377.suppl6